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Morphological variation and the definition of species in the snake genus *Tropidophis* (Serpentes, Tropidophiidae)

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Synopsis. Historically, the definition of species in the Neotropical snake genus *Tropidophis* has been difficult because of intraspecific variation in scalation and a paucity of specimens of most taxa. There were 13 species recognized at the time of the last review in 1960, but additional species have since been discovered and a taxonomic review and update is needed. Data on morphological variation are presented here and used to clarify the status of the described taxa. Because many taxa are allopatric with their closest relatives, it is necessary to make decisions as to their status as species or subspecies. As a gauge of species status in the genus, character divergence in ten pairs of closely related sympatric species was examined. Typically, such species are differentiated by two non-overlapping colour pattern differences, often in combination with a diagnostic (non-overlapping) or overlapping difference in scalation. Using this criterion, seven taxa previously considered as subspecies are here elevated to species status, whereas seven other taxa are retained as subspecies, although in some cases they are allocated to different species. As a result, the genus *Tropidophis* is considered here to comprise 29 species, 26 of which are West Indian and 15 of those are restricted to Cuba.

INTRODUCTION

Tropidophis are typically small, stout-bodied snakes of the family Tropidophiidae that occur in South America and the West Indies. This family is a member of the primitive snake Infraorder Henophidia (Underwood, 1967). As recognized here, there are 29 valid species of *Tropidophis* and all but three occur in the West Indies, where Cuba (15 species) is the centre of diversity (Table 1). They are nocturnal and feed mostly on sleeping lizards (especially *Anolis*), but also on frogs (especially *Eleutherodactylus*); other nocturnal snakes may impinge on *Tropidophis* ecologically. All are viviparous and most are terrestrial, although several Cuban species are arboreal and gracile in habitus. They exhibit a diversity of colour patterns that include spots (mostly), bands (saddles), and stripes. They have the unusual ability of being able to change their colouration, physiologically (Hedges, Hass & Maugel, 1989). Typically they are paler when active (at night) and dark while inactive. Species distributions tend to be greatly restricted, with species endemic to single islands or island banks, and often to small areas on an island. However, species density can be high, and as many as six species are sympatric in some areas of Cuba.

Historically, the taxonomy of *Tropidophis* has been difficult to study because of small numbers of specimens and a paucity of diagnostic characters. For example, two of the earliest described species, *T. maculatus* and *T. pardalis*, have been confused repeatedly. Boulenger (1893) and Stull (1928) commented on the confusion of these species by Cope (1868), whereas Schwartz and Marsh (1960) later commented on their confusion by Stull! Most of these early problems in *Tropidophis* taxonomy stemmed from the use of characters later found to be unreliable, such as the keeling of scales or hemipene morphology. It was not until Schwartz and Marsh (1960) assembled a large number of specimens and collected extensive data on proportions, scalation and pattern that the systematics of this genus became reasonably well known. Although it was a large study, it was not comprehensive because it omitted species related to *T. melanurus* and those placed by Schwartz (1957) in the *semicinctis* group. However, their success was in recognizing the utility of colouration and pattern characters, and that species diagnosis in this genus often requires consideration of multiple characters, some of which may not be individually diagnostic.

This is not a comprehensive revision of the genus but rather a taxonomic update, motivated by the many changes that have occurred since that last major review (Schwartz & Marsh, 1960) and the need to summarize what is known of morphological variation in the genus. Another motivation is to address a recurring problem in the systematics of this group: determining the species status of allopatric populations and taxa. In the process, taxa previously considered as subspecies are here elevated to species status, some are assigned to different species, and others are left unchanged.

MATERIALS AND METHODS

The data presented herein are almost entirely from the literature, or were used in published studies (but not necessarily published in the form here). Most derive from the raw data sheets of the late Albert Schwartz, used primarily in several publications (Schwartz, 1975; Schwartz & Garrido, 1975; Schwartz & Henderson, 1991; Schwartz & Marsh, 1960; Schwartz & Thomas, 1960; Thomas, 1963). Schwartz's Cuban specimens are in the American Museum of Natural History and his other material is almost entirely in the collection of the Museum of Natural History, University of Kansas. In addition to those data, I have included data from specimens I and colleagues have collected during the last two decades of field work, and which, for the most part, formed the basis of several published studies: (Hedges, Estrada & Diaz, 1999; Hedges & Garrido, 1992; Hedges & Garrido, 1999; Hedges & Garrido, 2002; Hedges, Garrido & Diaz, 2001). This material is in the National Museum of Natural History (Smithsonian) and in Cuban collections (National Museum of Natural History, Havana; Institute of Ecology and Systematics,

Table 1 Species, species groups, and distributions of snakes of the genus *Tropidophis*.

Species	Species Group	Distribution
T. battersbyi Laurent	taczanowskyi	South America
T. bucculentus Cope	melanurus	Navassa Island
T. canus Cope	melanurus	Bahamas
T. caymanensis Battersby	melanurus	Grand Cayman
T. celiae Hedges, Estrada, and Díaz	melanurus	Cuba
T. curtus Garman	melanurus	Bahamas
T. feicki Schwartz	maculatus	Cuba
T. fuscus Hedges and Garrido	pardalis	Cuba
T. galacelidus Schwartz and Garrido	pardalis	Cuba
T. greenwayi Barbour and Shreve	haetianus	Turks and Caicos
T. haetianus Cope	haetianus	Hispaniola
T. hardyi Schwartz and Garrido	pardalis	Cuba
T. hendersoni Hedges and Garrido	pardalis	Cuba
T. jamaicensis Stull	jamaicensis	Jamaica
T. maculatus Bibron	maculatus	Cuba
T. melanurus Schlegel	melanurus	Cuba
T. morenoi Hedges, Garrido, and Díaz	maculatus	Cuba
T. nigriventris Bailey	pardalis	Cuba
T. pardalis Gundlach	pardalis	Cuba
T. parkeri Grant	melanurus	Little Cayman
T. paucisquamis Müller	taczanowskyi	South America
T. pilsbryi Bailey	pardalis	Cuba
T. schwartzi Thomas	melanurus	Cayman Brac
T. semicinctus Gundlach and Peters	maculatus	Cuba
T. spiritus Hedges and Garrido	pardalis	Cuba
T. stejnegeri Grant	jamaicensis	Jamaica
T. stullae Grant	jamaicensis	Jamaica
T. taczanowskyi Steindachner	taczanowskyi	South America
T. wrighti Stull	pardalis	Cuba

Havana). In nearly all cases, museum numbers and localities of those specimens are listed in the publications and therefore are not repeated here.

In some cases, summary data presented in the tables of Schwartz and Marsh (1960) do not agree with those in the raw data sheets or with data mentioned in the text of Schwartz and Marsh, presumably because of typographical errors in their tables. Some of the data presented later in Schwartz and Henderson (1991), such as the ventral range of *T. canus* and caudal range of *T. maculatus*, appear to be derived from those typographical errors. Although these errors are minor, the summary data presented in this paper were taken directly from Schwartz's raw data sheets, to avoid any confusion, and supplemented with additional data. Also, some characters were not scored by Schwartz in some species (e.g., parietal contact in *T. feicki*, *T. melanurus*, *T. semicinctus*, etc) or at all (e.g., ratios of eye length to head width and head width to neck width, and aspects of colour pattern). In those cases, specimens at hand were examined to fill in the gaps. I have examined preserved material of most taxa, and have observed and collected 12 of the species: *T. canus, T. feicki, T. fuscus, T. greenwayi, T. haetianus, T. maculatus, T. melanurus, T. pardalis, T. pilsbryi, T. stejnegeri, T. stullae, and T. wrighti.*

Because this is not a comprehensive revision, there was no attempt to survey all collections for holdings of *Tropidophis* or to examine all available material. It is anticipated that such an undertaking will be attempted in the future.

RESULTS AND DISCUSSION

The conclusion of this taxonomic update is the recognition of 29 species of *Tropidophis* (Table 1). This is an increase of about six species over the number recognised earlier this year (Hedges & Garrido, 2002). The difference involves the elevation of some taxa previously considered as subspecies. Below, I discuss the utility of different characters used, my reasoning in determining species boundaries, and the taxonomic issues involved in each geographic area. The phylogeny and biogeography of species in this genus, using DNA sequence data, is discussed elsewhere (S. B. Hedges, S. C. Duncan, A. K. Pepperney, in preparation). The species group status (Table 1) is based on that work, but otherwise the focus of this current assessment is the definition of species boundaries, not phylogenetic relationships.

Characters

Variation in 20 characters among the 29 species of *Tropidophis* is shown in Tables 2–4. They are grouped into those involving proportions (Table 2), scalation (Table 3), and pattern and coloration (Table 4). In general, sexual dimorphism in *Tropidophis* is not pronounced and therefore data from both sexes can be combined, with the exception of body size, which shows slight differences. Characters that I have found to be of limited value have been eliminated. These include four that are commonly scored in snake systematics: upper and lower labials and the pre- and postoculars. All four are variable within species and in almost all cases, not diagnostic. Upper labials are usually 9–10 and lower labials usually 9–12 in all species. In *T. melanurus* and some related species, labial counts tend to be higher, although even in those cases there is often overlap. There is usually one preocular and 2–3 postoculars in *Tropidophis*, although some species occasionally have two preoculars and as many as 4 postoculars; however, variation in ocular scales does not appear to be of taxonomic utility. Examples of exceptions, as noted by Schwartz and Marsh (1960), are *T. pardalis* (usually 2 postoculars) and *T. maculatus* (usually 3 postoculars), although such differences are rarely diagnostic. Stull (1928) considered the forking of the hemipenis (bifurcate versus quadrifurcate) to be a diagnostic character but Schwartz and Marsh (1960) could not identify any species or specimens with a quadrifurcate condition. Also, such a character would not be very useful in this group because of limited material and scarcity of specimens with properly everted hemipenes.

Schwartz scored several other characters in *Tropidophis*, but I have also found them to be of limited value in diagnosing taxa. In the case of relative tail length (Schwartz & Marsh, 1960), it is useful in distinguishing *T. canus* from *T. curtus* (see below) but otherwise is difficult to score because of tail damage in some specimens, and overlapping of ratios. The colour of the tail tip (pale versus dark) was useful in distinguishing Cayman Islands *Tropidophis* from *T. melanurus* (Thomas, 1963), and other trends are noticeable, but differences between juveniles and adults, and intraspecific variability, make it a less useful character.

Now considering the 20 tabulated characters, maximum snout-vent length (SVL) is useful because some species differ greatly in body size, and most individuals encountered are adults. Two ratios (Table 2) that I have found to be of utility are eye length/head width (i.e., relative size of the eye) and head width/neck width (i.e., distinctiveness of the head). Both ratios are larger in the arboreal species *T. feicki*, *T. semicinctus*, and *T. wrighti*, and in another gracile Cuban species (*T. fuscus*) that is possibly arboreal (Hedges & Garrido, 1992). Unfortunately, both show variation within species and sample sizes still are small.

Despite the intraspecific variability in the scale characters (Table 3), some are useful when considered simultaneously with other characters. Ventral and midbody scale row counts are perhaps the most useful whereas caudal counts and posterior scale row counts are the least useful. Contact of the two parietal scales can be

Table 2 Variation in proportions of snakes of the genus *Tropidophis*.

Species	Max. SVL (mm) males	Max. SVL (mm) females	Eye diameter/ head width	Head width/ neck width	Sample size[1]	References[2]
T. battersbyi	na[3]	na	na	na	1	1
T. bucculentus	360	596	0.19–0.24 (2)	1.50–1.55 (2)	4	2–5
T. canus	363	338	na	na	20	2, 6
T. caymanensis	470	438	0.26 (1)	1.59 (1)	13	2–3, 7
T. celiae	na	344	0.28 (1)	1.31 (1)	1	8
T. curtus	357	354	0.25 (1)	1.35 (1)	93	2–3, 6
T. feicki	411	448	0.28–0.32 (4)	1.76–2.24 (4)	29	2–3, 9
T. fuscus	287	304	.30–.33 (2)	1.83–1.99 (2)	8	10–11
T. galacelidus	187	405	0.28 (1)	1.45 (1)	6	2–3, 6, 12
T. greenwayi	313	301	0.23 (1)	1.35 (1)	16	2–3, 6
T. haetianus	534	552	0.22–0.25 (8)	1.28–1.52 (8)	158	2–3, 6, 13
T. hardyi	303	334	0.26–0.31 (2)	1.30–1.49 (2)	8	2–3, 6, 12
T. hendersoni	302	315	0.28 (1)	1.45 (1)	1	14
T. jamaicensis	338	306	0.20–0.21 (3)	1.47–1.54 (3)	23	2–3, 6
T. maculatus	327	347	0.23–0.32 (5)	1.30–1.92 (5)	25	2–3, 6
T. melanurus	770	957	0.21–0.26 (8)	1.28–1.77 (8)	100	2–3, 15
T. morenoi	na	295	0.24–0.27 (2)	1.39–1.52 (2)	2	16
T. nigriventris	184	227	na	na	4	2, 6, 12
T. pardalis	264	287	0.24–0.27 (4)	1.26–1.63 (4)	161	2–3, 6
T. parkeri	422	512	0.24 (1)	1.95 (1)	21	2–3, 7
T. paucisquamis	101	283	0.24–0.28 (3)	1.53–1.71 (3)	3	2–3
T. pilsbryi	295	260	.24–.25 (2)	1.59–1.62 (2)	8	2–3, 6, 10
T. schwartzi	385	321	na	na	17	2–3, 7
T. semicinctus	383	408	0.30–0.34 (2)	1.70–1.88 (2)	26	2–3, 9
T. spiritus	320	372	0.24–0.37 (4)	1.35 (1)	4	17
T. stejnegeri	395	529	0.22–0.28 (3)	1.39–1.48 (3)	23	2–3, 6
T. stullae	260	248	0.23–0.25 (3)	1.78–1.86 (3)	4	2–3, 6
T. taczanowskyi	305[4]	243	0.27–0.30 (2)	1.46–1.51 (2)	3	3, 10, 18
T. wrighti	330	323	0.32–0.34 (7)	1.77–2.24 (7)	17	2–3, 9

[1]number of specimens used for most measurements and counts, unless otherwise indicated in parentheses.
[2]primary sources of the data reported in this and other tables: 1 (Laurent, 1949), 2 (Albert Schwartz, unpublished data), 3 (S. B. Hedges, unpublished data), 4 (Thomas, 1966), 5 (Bailey, 1937), 6 (Schwartz & Marsh, 1960), 7 (Thomas, 1963), 8 (Hedges *et al.*, 1999), 9 (Schwartz, 1957), 10 (Hedges & Garrido, 1992), 11 (Ansel Fong, unpublished data), 12 (Schwartz & Garrido, 1975), 13 (Schwartz, 1975), 14 (Hedges & Garrido, 2002), 15 (Schwartz & Thomas, 1960), 16 (Hedges *et al.*, 2001), 17 (Hedges & Garrido, 1999), 18 (Stull, 1928).
[3]data not available
[4]sex not determined

diagnostic in some comparisons (Hedges & Garrido, 2002), but problems arise in how different people score the character (e.g., when an interparietal is present and scales barely touch). As already noted, the keeling of the dorsal scales is often variable within species. Many species have weakly keeled scales that are noticeable only above the vent region and are difficult to score consistently, and depend sometimes on condition of preservation. However, some species consistently have smooth scales and others (e.g., *T. melanurus*) have distinctly keeled scales.

Colour and pattern variation (Table 4) has been important in *Tropidophis* taxonomy, in part because the snakes are frequently spotted and this provides yet additional characters to count. In fact, Schwartz and Marsh (1960) considered coloration and pattern to be the most reliable characters, in combination with scalation, for 'separating and combining' taxa. Except for *T. feicki*, which has crossbands, most species have 2–12 rows of body spots. I have used the Schwartz and Marsh (1960) methods of scoring body spots and spot rows. Spot rows include those on the dorsum and venter, all around the body (both sides) whereas body spots are counted along one row of spots (usually just to one side of middorsal region) from behind the head to just above the vent. Typically, the largest and most distinctive spots are those near the middorsal region. This reaches an extreme in species of the *melanurus* group where some individuals have only those two spot rows present, resulting in widely varying row counts (e.g., 2–10). Occipital spots sometimes fused to form a white neckband, are diagnostic of several species (e.g., *T. celiae, T. galacelidus, T. pilsbryi, T. stejnegeri*) and are common in others (e.g., *T. pardalis*).

The dorsal ground colour of most species is a shade of brown or grey, and often variable within species. I once collected two specimens of *T. pilsbryi* in the same rock pile in Cuba, and was initially misled into thinking they were different species because one was brown and the other grey. On the other hand, *T. stullae* is consistently pale tan and differs from the other two Jamaican species, which are darker. Also, two boldly spotted species that occur sympatrically in western Cuba can be distinguished by, among other things, their dorsal ground colour: greyish pink in *T. feicki* and yellow to orange in *T. semicinctus*. Although most species are spotted, those in the *melanurus* group often have narrow lateral stripes as well as a middorsal stripe. The absence of middorsal spot contact occurs in two related species, *T. maculatus* and *T. semicinctus*, and the two Bahaman species *T. canus* and *T. curtus* are united by the presence of an anteriolateral (face and neck) stripe. Ventral pattern is diagnostic for *T. nigriventris* (almost completely dark) and in several species that lack a ventral pattern, but otherwise most have different degrees of spotting and flecking.

Species boundaries

Most taxonomists discern the presence of sympatric species by covariation of multiple characters from individuals of a single locality, indicating lack of gene flow between the species. For example, in a series of dark and pale snakes found together, two species would be indicated if all of the dark snakes also had small

Table 3 Variation in scalation of snakes of the genus *Tropidophis*. (Numbers and character states in brackets represent rare or infrequent occurrences; Y = yes, N = no; other notation as in Table 2.

Species	Ventrals	Caudals	Dorsal scale rows			Parietal contact	Keeled dorsals
			Anterior	Midbody	Posterior		
T. battersbyi	200	41	21	23	17	N	N
T. bucculentus	183–186	28–32	24–25	25–27	17–19	N	Y
T. canus	170–183	29–35	21[20,22,23]	23[22]	16–21	N/Y	Y[N]
T. caymanensis	183–200	33–38	23–27	23[25]	17[19]	N	N/Y
T. celiae	203	30	25	27	19	Y	N
T. curtus	146–173	22–37	19–27	23–25	17–22	N[Y]	Y[N]
T. feicki	217–235	34–41	23–25[19,21]	23–25	17–19	N/Y	N
T. fuscus	160–185	30–36	21–24	23	15–19	N	Y
T. galacelidus	177–186	29–35	25–27	25–27	19–20	N	Y
T. greenwayi	155–165	26–30	23–25	25–27	17–19	Y	N
T. haetianus	170–194	27–39	23–27	25–27[23,29]	17–19[21]	Y[N]	N
T. hardyi	153–172	31–48	20–24	23–25	18–20	N/Y	N/Y
T. hendersoni	190	33	23	25	19	N	Y
T. jamaicensis	167–181	28–36	23–27	25–29	15–23	N/Y	N
T. maculatus	189–208	28–40	22–25	25[23]	17–21	N/Y	N/Y
T. melanurus	188–217	31–44	24–27[19]	27–29 [24,25,26,30]	17–21 [16,22,23,24]	N	Y
T. morenoi	198–199	42–44	23	23	17	N	N
T. nigriventris	144–150	25–26	23–25	23–25	18–22	N	N
T. pardalis	140–157	23–34	21,23 [19,22,24,25]	23,25 [21,22,24]	17–21[16]	N/Y	N[Y]
T. parkeri	199–212	33–41	25[23,24]	27[25,26]	17[18,19]	N	Y
T. paucisquamis	170–178	37–40	21	21	17	Y	N
T. pilsbryi	160–169	26–31	22–25	23–25	17–21	N	N/Y
T. schwartzi	191–205	31–39	25	25[26]	17[15]	N	Y
T. semicinctus	201–223	33–41	21,23[22,24,25]	25[21–24]	17–20	N/Y	N
T. spiritus	183–200	35–39	21–23	23	17	N	N
T. stejnegeri	181–190	30–38	25–27[23]	25,27[26]	17–19	N/Y	Y
T. stullae	166–170	31–34	25	25	16–19	N	N
T. taczanowskyi	149–160	25–27	23–25	23	19–21	Y	Y
T. wrighti	192–215	36–45	21–23	21–23	17[16,18,19]	N	N

heads and fewer spots than the pale snakes (thus, body colour would be covarying with head size and spot number). In the case of allopatric populations, it is typically assumed that character differences similar to or greater than observed between sympatric species indicate that the two forms are different species. Thus, the 'yardstick' used for assessing allopatric populations is character divergence between closely related, sympatric species. This is the principle that I use here in assessing species status within *Tropidophis*. It is a practical species concept but is based on the observation that species are reproductively isolated from each other, as noted by Darwin (1859) and later articulated by Mayr (1942) as the *biological species concept*.

The reason that a particular degree of differentiation is necessary, rather than a minimal diagnostic difference, concerns the 'reality' of species in evolution. Almost all species are fragmented (structured) to some degree, and many populations can be diagnosed by one or a few nucleotide differences or minor morphological differences. However, through time, such populations frequently combine and separate again as part of the reticulate nature of gene flow and evolution within species. It is only those populations that have differentiated sufficiently, genetically and/or morphologically, and presumably reflecting a length of time, that evolve reproductive isolation from other populations. Thus, to assign species status to diagnosable, but ephemeral, populations during one slice of time is arbitrary from an evolutionary standpoint. Although Frost and Hillis (1990) recommended abandoning the use of quantitative criteria (molecular and morphological) for discerning species status of allopatric populations, they did not propose anything to replace that procedure and thus few have heeded their recommendation.

Sympatric species of *Tropidophis* occur only in Cuba. In western Cuba, the following six species have been found in the general region of Canasí, Habana Province: *T. celiae, T. feicki, T. maculatus, T. melanurus, T. pardalis, and T. semicinctis*. In central Cuba, the following six species have been found in the vicinity of the Trinidad mountains: *T. galacelidus, T. hardyi, T. melanurus, T. pardalis, T. semicinctis, and T. spiritus*. In eastern Cuba, the following four species are known from the region of Baracoa, Guantánamo Province: *T. fuscus, T. melanurus, T. pilsbryi, and T. wrighti*. To identify the level of character divergence associated with species differentiation in *Tropidophis*, I now focus on four clusters of sympatric species, each of which are members of the same species group: (1) *feicki/maculatus/semicinctis*,(2) *celiae/melanurus*, (3) *pardalis/galacelidus/hardyi, and* (4) *fuscus/wrighti/pilsbryi*.

In cluster (1), *T. maculatus* and *T. semicinctis* are closest relatives according to DNA sequence evidence (S. B. Hedges, S. C. Duncan, A. K. Pepperney, in preparation) and are distinguished primarily by colour pattern: the number of body spots (no overlap) and number of spot rows (no overlap). All scale counts in those two species overlap, although *T. semicinctis* tends to have a higher number of ventrals. In the case of *T. feicki* and *T. maculatus*, there are non-overlapping differences in ventral counts, body spots, and spot rows. Considering *T. feicki* and *T. semicinctis*, the ground colour and spot rows are non-overlapping, and the ventral counts are different but overlap slightly.

In cluster (2), *T. celiae* and *T. melanurus*, which are close relatives according to DNA sequence evidence, completely overlap in all scale counts, although parietal contact might be considered diagnostic if there were more than one specimen of *T. celiae*. Otherwise,

Table 4 Variation in pattern and colouration of snakes of the genus *Tropidophis*. (Numbers and character states in brackets represent rare or infrequent occurrences; Y = yes, N = no; other notation as in Table 2.

Species	Body spots	Tail spots	Spot rows	Occipital spots	Dorsal ground colour	Dorsal pattern	Stripe: Anterio-lateral	Stripe: Mid-dorsal	Mid-dorsal spot contact	Ventral pattern
T. battersbyi	na	na	6	na	Pale brown	spots	N	na	na	spotted
T. bucculentus	48–54	5–7	6	N	pale ashy brown	spots and stripes	N	N	Y	spotted or not
T. canus	43–59	3–7	6,8[7,9]	N	pale greyish yellow	spots and stripes	Y	N	Y	speckled
T. caymanensis	48–61	5–9	2–10	N	pale grey and cream	spots and stripes	N	Y	Y	speckled
T. celiae	60	12	6	Y	pale tan	spots	N	Y	Y	none
T. curtus	38–90	2–13	10[8,9,11,12]	N	greyish brown	spots and stripes	Y	N/Y	Y	spotted or not
T. feicki	17–26	2–6	1	N	grey or pink	saddles	N	N	Y	none
T. fuscus	43–52	na	6–8	N/Y	dark brown	spots	N	N	Y	spots
T. galacelidus	44–50	4–9	10	Y	grey	spots	N	N/Y	Y	spots
T. greenwayi	27–49	3–6	10[8]	N	dark brown	spots and broken lines	N	N	Y	spots
T. haetianus	36–61	0–13	8–10[6]	N	brown or tan	spots	N	N	Y	none or stippled
T. hardyi	32–44	4–6	6–8	N	medium brown	spots	N	N	Y	spotted
T. hendersoni	48–52	7–8	10	Y	tan	spots	N	N	Y	unpatterned
T. jamaicensis	38–54	4–10	6–10	N	chocolate brown	spots	N	N	Y	spots
T. maculatus	35–55	4–11	8–10	N	red or reddish tan	spots	N	N	N	spots
T. melanurus	47–54 (20)	5–7 (3)	2–10	N	tan or brown	spots and stripes	N	Y	Y	stippling
T. morenoi	38–39	4–8	6	N	whitish beige	narrow bands	N	N	Y	spots
T. nigriventris	37–46	4–5	8	N	Brown	spots	N	N	Y	dark brown
T. pardalis	25–42	3–7	6[8]	N/Y	tan to brown	spots	N	N	Y	spots
T. parkeri	40–62	4–6[8]	2–10	N	pale grey and tan	spots and stripes	N	Y	Y	speckled
T. paucisquamis	25–26	0	6–8	na	Brown	spots	N	N	na	spots and bands
T. pilsbryi	36–48	4–8	8–10	Y	grey or brown	spots	N	N	Y	spots
T. schwartzi	49–64	5–9	2–10	N	pale grey and cream	spots and stripes	N	Y	Y	speckled
T. semicinctus	18–29	3–9	2	N	yellow to orange	spots	N	Y	N	none
T. spiritus	36–42	3–6	6	N	greyish tan	spots	N	N	Y	spots
T. stejnegeri	36–57	4–11	8–10	Y	Yellowish grey	spots	N	Y	Y	spots
T. stullae	43–54	5–8	10[4]	N	pale tan	spots	N	Y	Y	spots
T. taczanowskyi	na	0	8	N	brownish violet	spots and stripes	N	N	na	spots and bands
T. wrighti	21–37	3–6	4	N	white or tan	spots	N	N	Y	spots

about the only characters that distinguish these two species are body size and aspects of coloration (e.g., neckband in *T. celiae* and higher number of body spots). In case the reader is wondering, the presence of enlarged ova in the small holotype of *T. celiae*, and details of the pattern, indicate it is not a juvenile *T. melanurus* (Hedges *et al.*, 1999).

In cluster (3), there are no molecular data available for *T. galacelidus* and *T. hardyi* to confirm their species group association with *T. pardalis*. However the association is supported by the fact that there are no diagnostic (non-overlapping) scale or pattern characters that distinguish *T. hardyi* and *T. pardalis*. This problem was noted in the original description (Schwartz & Garrido, 1975). However, *T. hardyi* has a higher number of ventrals, even though overlapping with *T. pardalis*, and it is a larger species with a distinctly smaller head. The latter character caused Schwartz and Garrido to associate (as a subspecies) *T. hardyi* with the small-headed *T. nigriventris*. The third sympatric species of this trio, *T. galacelidus*, can be distinguished from the other two species by its higher number of ventrals, dorsal spots, and spot rows (all non-overlapping).

In the case of cluster (4), DNA sequence evidence place all three together as close relatives. *Tropidophis fuscus* and *T. pilsbryi* have no completely diagnostic scale differences, although the combination of ventral scale counts and midbody scale rows will distinguish the species. Also, *T. fuscus* has a more gracile body shape. The third species, *T. wrighti*, is diagnosed from the other species by its higher ventral counts, and fewer dorsal spots and spot rows (all non-overlapping).

To summarize, of the ten combinations of closely related, sympatric species, nearly all were distinguished by at least two non-overlapping differences in colour pattern, or (less frequently) body proportions. In addition, there was usually one other difference (either non-overlapping or overlapping) in scalation. More distantly related species of *Tropidophis* often have two (or more) non-overlapping differences in scalation, in addition to any other differences. This suggests a temporal sequence in character differentiation, with colour pattern and body proportion differences accruing first, followed by scalation differences. Ideally, one would like to use molecular data as well for assessing differentiation, although tissue samples still are not yet available for many taxa. Using this morphological criterion for assessing species status in *Tropidophis*, I will now review the current status of the taxa in this genus.

Hispaniola

Only one species (*T. haetianus*), with three subspecies, occurs on Hispaniola: *T. h. haetianus* (most of island), *T. h. hemerus* (distal portion of the Tiburon Peninsula in Haiti) and *T. h. tiburonensis* (extreme eastern portion of the Dominican Republic). Although Schwartz and Marsh (1960) and Schwartz (1975) have considered the Jamaican taxa to be subspecies of *T. haetianus*, genetic evidence has shown that they are more closely related to the Cuban species (Hass, Maxson & Hedges, 2001) and thus are removed from *T. haetianus* (see below). Also, the Cuban specimens of *T. haetianus* discussed by Schwartz and Marsh (1975) and Schwartz and Garrido (1975) have been removed from that species and assigned to a new species, *T. hendersoni* (Hedges & Garrido, 2002). Because the subspecies of Hispaniolan *T. haetianus* are parapatric and apparently intergrade (Schwartz, 1975), and because their character differentiation is less than that of sympatric species, I suggest retaining their current taxonomic status as subspecies. It is possible that genetic studies in the future may further clarify their status. Thus, *T. haetianus* is confined to Hispaniola and contains three subspecies.

Navassa Island

Four specimens of *T. bucculentus* are known from this small island between Hispaniola and Jamaica, but apparently no snakes have been seen in over 100 years and thus the species is considered extinct (Powell, 1999). Since it was described by Cope (1868), there has been considerable confusion as to its species status and relationship with other species. Most who have examined the type series, including me, have noted a resemblance to *T. melanurus* (Thomas, 1966), although Stull (1928) instead considered it a subspecies of *T. pardalis*. There is no overlap in ventral counts between *T. bucculentus* and *T. melanurus*, and almost no overlap in caudal counts. Although there appear to be pattern differences between the two species, the single specimen in the Academy of Natural Sciences (Philadelphia) differs from the other three specimens (National Museum of Natural History, Smithsonian) in terms of ventral pigmentation (Bailey, 1937). Based on the diagnostic scalation differences alone, I would consider *T. bucculentus* as a valid species. The unusual geographic location of a species with apparent Cuban affinities, on Navassa Island, is remarkable. With the exception of the anole (*Anolis longiceps*), other species on Navassa have affinities with nearby Hispaniola (Powell, 1999; Thomas, 1966), which is logical based on the westerly direction of ocean currents. However, the eastern tip of Cuba is further east than Navassa, and ocean currents flow southerly through the Windward Passage separating Cuba and Haiti. Dispersal on those currents is thus possible and is the most likely explanation for the origin of *T. bucculentus* (and *A. longiceps*) on Navassa and possibly the gecko Sphaerodactylus notatus on the Morant Cays southeast of Jamaica. The locally changing direction of water currents during a hurricane may also have aided in the dispersal of these taxa.

Cuba

With 15 described species, Cuba is the hot spot of species diversity in the genus. Recently, two subspecies described by Schwartz and Garrido (1975) were elevated to species status and a new species was described from eastern Cuba (Hedges & Garrido, 2002). Character differences among many of the Cuban species have been discussed above (see 'Species Boundaries'), and I consider all 15 species to be valid. Also, I am aware of material that likely represents additional, undescribed species. Undoubtedly, more species will be discovered.

Two remaining taxa are considered subspecies of *T. melanurus*: *T. m. dysodes* and *T. m. eriksoni* (Schwartz & Thomas, 1960). The former is known from three female specimens from near La Coloma, Pinar del Rio Province, and the latter is restricted to Isla de Juventud. These taxa differ from *T. m. melanurus* primarily in size of the dorsal spots and in having bolder, darker colouration, with *T. m. dysodes* having the darkest pigmentation of the three subspecies. The ventral counts of *T. m. eriksoni* are low for the species, but there is considerable overlap with the other two taxa. Considering that there are no diagnostic differences in body proportion or scalation, and the colouration differences, although real, are not as trenchant as those distinguishing sympatric, closely related species (e.g., *T. maculatus* and *T. semicinctis*), I am inclined to leave their status as subspecies unchanged until additional data warrant a reconsideration.

Jamaica

The three Jamaican taxa, originally described as full species, are closer to Cuban taxa than to *T. haetianus* based on immunological data (Hass *et al.*, 2001) and DNA sequence data (S. B. Hedges, S. C. Duncan, A. K. Pepperney, in preparation). However, they form a

single genetic and morphological group (*jamaicensis* group), and are distinguished morphologically from the Cuban species at the species level, although they are closest to species of the *pardalis* group. The question then remains as to whether they should be treated as a single species (*T. jamaicensis*) or three separate species: *T. jamaicensis*, *T. stejnegeri*, and *T. stullae*. However, using the morphological criterion for species status, I recommend the latter. Each of these three taxa can be diagnosed based on scalation, body proportions, and colour pattern, and they are as different from each other as sympatric species in Cuba. In body size, *T. stejnegeri* (529 mm SVL) is considerably larger than *T. stullae* (260 mm SVL), with *T. jamaicensis* (338 mm SVL) being intermediate in size. Ventral counts of *T. stejnegeri* do not overlap with those of *T. stullae*, and counts of *T. jamaicensis* are nearly completely non-overlapping with the other two taxa. *Tropidophis stejnegeri* has keeled scales and occipital spots whereas the other two taxa are smooth scaled and lack occipital spots. Additionally, dorsal ground colours differ, being yellowish-grey (*T. stejnegeri*), chocolate brown (*T. jamaicensis*) and pale tan (*T. stullae*). A middorsal stripe is present in *T. stejnegeri* and *T. stullae* but absent in *T. jamaicensis*. The head of *T. stejnegeri* is pointed but that of *T. stullae* is distinctly squared-shaped.

The Bahamas Bank

Six taxa are currently recognized from the Bahamas Bank: *Tropidophis canus androsi* Stull (Andros Island), *T. c. barbouri* Bailey (central Bahamas, from Eleuthera to Ragged Island), *T. c. canus* Cope (Great Inagua), *T. c. curtus* Garman (New Providence, Bimini Islands, and Cay Sal Bank), *T. g. greenwayi* Barbour and Shreve (Ambergris Cay), and *T. g. lanthanus* Schwartz (Caicos Islands). Schwartz and Marsh (1960) considered all except the last two to be subspecies of a single species (*T. canus*) and that arrangement has since been followed. However, it is worth reviewing morphological variation in *T. canus* in the context of our current understanding of species definitions in the genus. Recent evidence from DNA sequences has shown that *T. greenwayi* is most closely related to *T. haetianus* (Hispaniola) and unrelated to the complex currently considered under *T. canus*.

Among the four subspecies of *T. canus*, *T. c. canus* stands out both morphologically and geographically. It is isolated in the south, being separated from the northern taxa by islands apparently lacking *Tropidophis*: Crooked, Acklins, Mayaguana, and Little Inagua. It has a higher number of ventrals (170–183). One specimen (1%) of the northern group has 173 ventrals; all others have fewer than 168 ventrals. Anterior and midbody scale rows in *T. c. canus* typically are 21–23 whereas they are typically 23–25 in the northern taxa, although there is some overlap. The tails of *T. c. canus* are distinctly shorter, averaging 11% (9.4–12.1), compared with 13% (11.0–15.2) in the northern taxa. Rows of body spots number 6–8 in *T. c. canus* whereas they are typically 10 or more in the northern taxa; overlap consists of nine specimens (10%) of northern taxa with eight rows and two (2%) with nine rows, and one (5%) *T. c. canus* with nine rows. This degree of difference is the same or greater than that seen between sympatric species of *Tropidophis* in Cuba, and therefore the northern taxa should be removed from *T. canus*.

The status of the three northern Bahaman taxa is problematic at this time. Clearly there is geographic variation among these forms. For example, *androsi* tends to have a higher number of ventral scales than the other two taxa, although there is considerable overlap with *barbouri* and some with *curtus*. Within one taxon (*curtus*), snakes from Bimini are distinctly larger than those from New Providence. Both Bailey (1937) and Schwartz and Marsh (1960) noted very little difference, overall, between *barbouri* and *androsi*. When considering the 'species boundary' characters noted above, there is insufficient justification at present to recognize these taxa as distinct species. Additional specimens and genetic analyses will be necessary to better resolve geographic variation in northern Bahaman *Tropidophis*. Until then, I suggest here that *androsi* and *barbouri* be recognized as subspecies of *T. curtus*: *T. curtus androsi* (new combination) and *T. curtus barbouri* (new combination).

Tropidophis greenwayi lanthanus is a subspecies found in the Caicos Islands and is distinguished by coloration difference from the nominate subspecies on nearby Ambergris Cay (Schwartz, 1963). However, the difference concerns 'interspace stippling' and not actual numbers of spots or spot rows. There are no diagnostic scale count differences, and the presence of two postoculars in the two known specimens of *T. g. greenwayi* is not remarkable because half of the specimens of *T. g. lanthanus* also have two postoculars, at least on one side of the head. More material of *T. g. greenwayi* is needed, in addition to genetic analyses, before the species status of *T. g. lanthanus* can be accurately assessed. I suggest that the latter taxon continue to be recognized as a subspecies.

Thus, *Tropidophis* of the Bahamas Bank are placed here in three species: *T. greenwayi* (Turks and Caicos), *T. canus* (Great Inagua), and *T. curtus* (northern and central Bahamas). The question as to whether some Bahaman species also occur in Cuba has been raised in the past, primarily because of two old specimens (Schwartz & Marsh, 1960). The first is the type of *T. curtus*, purportedly from 'Cuba' (Garman, 1887). However, morphologically it agrees with snakes from New Providence, Bahamas, and the specimen number (MCZ 6114) is close to other numbers in that collection from New Providence. Also, the origin of the specimen was investigated and found to be 'without definite history' (Stull, 1928). Thus, I agree with Stull in considering this specimen to be from New Providence. The other specimen is AMNH 2946 from 'Nuevitas, Cuba' (no other information). As noted by Schwartz and Marsh (1960) it agrees in morphology with snakes here considered as *T. curtus*. Although they considered the provenance of the specimen to be correct, partly because of the confusion surrounding the holotype, I raise the question here that it also may be an error. The specimen number is close to several *T. curtus* from Andros Island (AMNH 2925–2927) apparently cataloged at about the same time and its scale counts fall within the range of counts of snakes from that island. Thus I consider the range of *T. curtus* to be restricted to the Bahamas.

The Cayman Islands

Currently there are three subspecies of *T. caymanensis* recognized from the Cayman Islands (Thomas, 1963) and they differ in scale row counts, ventral counts, and colour pattern. Each is endemic to a single island, and there is no evidence of intergradation. At the time they were last reviewed (Thomas, 1963), a more conservative definition of species boundaries in the genus prevailed. Although no new material has been examined here, the level of differences seen among these taxa would suggest that they are distinct species. *Tropidophis caymanensis* (Grand Cayman) is distinguished from *T. parkeri* (Little Cayman) by its lower anterior and midbody scale rows (23–25 versus 25–27), lower number of ventrals (183–200 versus 199–212), and a larger, darker cephalic pattern. *Tropidophis caymanensis* is distinguished from *T. schwartzi* (Cayman Brac) by its larger body size (maximum SVL = 470 mm versus 385 mm), lower anterior scale rows (23 versus 25), lower, albeit overlapping, number of ventrals (183–200, $\bar{x}$ = 192, versus 191–205, $\bar{x}$ = 198), fewer tail spots (4–8, mode = 6 versus 5–9, mode = 8) and a larger, darker, cephalic pattern. *Tropidophis parkeri* is distinguished from

T. schwartzi by its higher midbody scale rows (27 versus 25), higher number of ventrals (199–212, $\bar{x} = 203$ versus 191–205, $\bar{x} = 198$), and a larger, darker cephalic spot (Thomas, 1963).

South America

Although Stull (1928) and Schwartz and Marsh (1960) attempted to relate one or more of the South American taxa to West Indian species groups, I do not envision a close relationship. For example, the keeling of the dorsal scales in *T. taczanowskyi* is greater than I have seen in any West Indian taxon. In the case of *T. paucisquamus*, the low number (21) of midbody scale rows and a distinctive pattern of middorsal stripe and blotches is not like any West Indian species, as noted by Schwartz and Marsh (1960). The only known specimen of *T. battersbyi* has been described only as having six rows of spots, including two rows on the venter (Laurent, 1949; Pérez-Santos & Moreno, 1991). The fact that the venters of *T. paucisquamus* and *T. taczanowskyi* have both been described as consisting of black and yellow spots and bands (Stull, 1928) is noteworthy; such a pattern and colouration is not known in West Indian taxa. This might also suggest a relationship at least between these two species. Molecular phylogenetic evidence (S. B. Hedges, S. C. Duncan, A. K. Pepperney, in preparation) places *T. paucisquamus* outside of the West Indian clade, reinforcing the morphological distinction. Examination of additional specimens, and genetic data from *T. battersbyi* and *T. taczanowskyi*, are needed to clarify the relationships of these South American species. Until then, available evidence supports the placement of the South American species in a separate species group (*taczanowskyi* group).

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